XXVIII. *Observations on the Structure of the Seed and Peculiar Form of the Embryo in the* Clusiaceæ. *By* John Miers, *Esq., F.R.S., F.L.S. &c.*

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THE object of this paper is to present to the notice of the Linnean Society some remarks upon the seed of the *Clusiaceæ*, and to call the attention of botanists more especially to the structure of its embryo, the nature of which has been hitherto quite misunderstood. During my residence in Brazil, I made several observations upon the plants of this family: the many novel facts thus collected have since induced me to extend this inquiry, with a view of determining the true affinities and limits of the Order, and of establishing the characters of its several genera, concerning which our present data are greatly confused and imperfect. The evidence upon these more general points will, however, be reserved for a future occasion; my attention, as a matter of primary importance, being first confined to a consideration of the seminal structure of the family.

The earliest description of these features I find in Jussieu's 'Genera Plantarum,' p. 255, published in 1789, where, in his ordinal character of the *Guttiferæ*, he simply states that its embryo is erect, without albumen, and with hard corky cotyledons (lobis suberoso-callosis).

The next mention is in 1791, by Gærtner, who in his justly celebrated work 'De Fructibus,' &c., plate 105, figures, with his usual fidelity, his analysis of three species of *Garcinia*; these he describes (vol. ii. p. 105) as having a coriaceous testa, a thin integument, and a fleshy solid nucleus, which exhibits in its axis an apparently different development of a terete, sometimes compressed, lanceolate form, the whole nucleus constituting a compact inseparable mass: from these facts, contrary to the opinion of Jussieu, he infers that the great body of the nucleus is a large albumen, and that the axile portion is a pseudo-mono-cotyledonous embryo, closely united together in one solid body.

Richard in 1811, in his excellent memoir on Endorhizal embryos *, in order to mark the difference between the embryonal structure of the Monocotyledones, and certain peculiar macropodal forms observed in the seeds of some dicotyledonous plants, described and figured the structure of the embryos of *Pekea* (*Caryocar*) *tuberculosa* and *Clusia palmicida*. The former has been copied in every botanical work published since that time, in order to serve as an example of that peculiar development, but the latter has never been alluded to, or mentioned, in any such work, that I can find; indeed the fact appears to have escaped the recollection of every botanist who has written upon Guttiferous plants, except Jussieu, although it would have been important to have borne that circumstance in remembrance. Richard there correctly describes the seed of *Clusia* as being enveloped in pulp; one extremity of its brittle testa is pierced with an aperture, beneath which the nucleus exhibits a small protuberance cleft in two, which he states to be two minute cotyledons, the principal mass of the embryo being an enormous radicle; he points out the existence of an inner integument, one end of which is attached to

* Ann. du Mus. xvii. 456. tab. 9 & 10.

the aperture in the extremity of the testa, the whole nucleus forming, in his own peculiar technology, "an epispermic antitropal embryo." There is, however, one essential error in this otherwise correct description; like other botanists, he has mistaken the base for the apex of the seed.

Jussieu, in 1813, in a memoir upon the characters of the *Hypericinæ* and *Guttiferæ*, drawn from the structure of their seeds*, observes, that if the remarkable fact above recorded by so accurate an observer as Richard, be exact, *Clusia* cannot belong to *Guttiferæ*, but must constitute the type of a distinct family nearer to the *Marcgraaviaceæ*.

Choisy, in 1822, in a memoir upon the family of the *Guttiferæ*†, ascribes in its ordinal character features altogether different from those of Jussieu, and equally opposed to the description of Gærtner. He states that the seeds are without albumen, that the embryo is erect, and that the cotyledons are large, fleshy, either separable or combined in one mass. In *Garcinia*, he says, the seeds are arillate, and the cotyledons thick and conjoined; but in *Clusia* he declares that these presumed cotyledons are separable, a feature that no succeeding botanist has verified. He alludes in no way to the very different structure recorded by Richard, of the seed in *Clusia*, although, when he stated the separability of the cotyledons in that genus, this idea may probably have been derived from some indistinct recollection of the analysis of that eminent carpologist.

The description of the *Guttiferæ* in DeCandolle's celebrated 'Prodromus' (1824) is confessed to be a mere recapitulation of the above-mentioned memoir, and consequently the same characters are there repeated upon the authority of Choisy.

Cambessèdes, in a very able essay upon this Natural Order, and on its relation to the *Ternstrœmiaceæ*, published in 1828 ‡, affirms that throughout the family of the *Guttiferæ* "l'embryon est droit, les cotyledons sont grands, épais, très entiers, soudés ensembles; la radicule est très petite, en forme de mamelon; sa direction, relativement au point d'attache de la graine, mérite la plus grande attention, et démontre jusqu'à l'évidence, que dans les familles les plus naturelles, les caractères, considérées dans la plupart des cas comme de la première valeur, peuvent varier dans les genres d'ailleurs extrêmement voisins. Dans le *Clusia Criuva*, dont je possède des graines dans un état parfait de maturité, la radicule est tournée vers l'extrémité de la graine la plus éloignée du point d'attache." I shall presently demonstrate that this statement is founded on error, and that the inferences above drawn are illusory. In that memoir the embryos of *Clusia* and *Calophyllum* are described as being erect, inverted, the small mammæform point, which he calls the radicle, as being at the apex or opposite extremity to the basal hilum of attachment; while in those of *Mammea* and *Mesua*, the radicle is said to be small, and pointing in a contrary direction, that is to say, to the basal point of attachment. He therefore erroneously concludes, that in this family the embryo is either homotropal or antitropal, or in other words, that the radicle is sometimes directed to that point of the seed next the hilum, at others, towards the opposite extremity. It is, however, fair to mention that he had not confidence in the correctness of these observations, and stated his doubts on this point, for the guidance of future botanists.

* Ann. du Mus. xx. 463. † Mém. Soc. Phys. de Genève, tom. i. ‡ Mém. du Mus. xvi. 369.

In the following year M. Cambessèdes minutely described the several Guttiferous plants collected by M. Aug. St. Hilaire, in his journeys through Brazil (Flor. Bras. Merid. i. 314 *et seq.*), and there, in his character of *Clusia Criuva*, he thus defines its seminal features: "raphe ab hilo ad basin seminis ducta parùm elevata; radiculâ brevissimâ, mammæformi, basin seminis hilo contrariam spectante, cotyledonibus coalitis apicem seminis hilo proximum spectantibus." Little dependence, however, can be placed upon this ample and precise definition, especially in regard to the terms *base* and *apex*, because, as I shall have occasion to show, in the figures 8, 9 and 10 of plate 65 of the work referred to, the seed is placed in a position diametrically opposite to that in which it is attached to the placenta, as the point he there assumes to be the radicle is said to be *inferior*, and the stipitate or basal support is there represented as an arillus that covers the *apex* of the seed. It is necessary to bear these circumstances in remembrance, as there is here an evident misconception of the whole structure.

Prof. Kunth, in his details of the several Guttiferous plants collected in the Voyage of Humboldt and Bonpland, throws no light whatever on this portion of the subject.

Doctor Von Martius, in his admirable work (Nov. Gen. et Spec. Pl. Bras.), offers no account, either in his generic or specific descriptions, of the several Guttiferous plants there enumerated, as far as regards the nature of the seed; but he gives ample details of a plant resembling his *Clusia insignis*, and named by him *Platonia insignis*, figuring at the same time the analysis of its fruit and seed. The nucleus enclosed within the testa is there described to consist of a large mass of fleshy albumen, containing numerous oil-cells, and enclosing in its centre a long terete or club-shaped embryo, with a superior radicle, the whole consolidated into one integral inseparable mass. As this form of embryo, and the presence of copious albumen, were facts opposed to the generally received conclusion of botanists, in regard to the structure of the seed in *Clusiaceæ*, he suggested the propriety of placing his new genus *Platonia* in a distinct family, which he proposed to call *Canellaceæ*, thus associating it with the little-known *Canella alba*, a plant greatly differing from it in habit and floral structure, and of which we possess an imperfect knowledge, especially of its carpological features.

Endlicher, in his 'Genera Plantarum,' gives the characters of the Order and of each genus of the *Clusiaceæ*, in accordance with the views of Cambessèdes, and arranges *Platonia*, after Von Martius, in the *Canellaceæ*, as a suborder of the *Guttiferæ*.

Pöppig, in his 'Nova Genera et Species,' although he details the characters of several genera and species of Guttiferous plants from Peru and Northern Brazil, and figures some of them, does not enter into any description of the structure of the seed.

Prof. Lindley, in his 'Vegetable Kingdom,' where he gives an outline of the ordinal characters of the *Clusiaceæ*, adopts the views of Cambessèdes in regard to the nature of the seed, notwithstanding that he admits *Platonia* as a member of the family.

Prof. Miquel, giving in 1844 a detailed account of a species of *Arrudea* (Linn. xviii. 232), follows the example of Cambessèdes in misconceiving the structure of the seed, for he describes the embryo as having fleshy plano-convex cotyledons, and a very short radicle.

Lastly, M. Choisy, in a more recent memoir (1850) * on the *Guttiferæ* of India, and

* Mém. Soc. Phys. de Genève, tom. xii. p. 381.

some little-known American plants of this Order, gives many interesting observations on the organography, affinities and subdivisions of the family, as a prelude to a review of the various genera and differential characters existing between them. It is, however, singular, that in a memoir of such length, where he discusses fully the general structure of the Order, he does not make the smallest allusion to the important question of the nature of the seed, concerning which so many uncertainties and incongruities are known to exist: this is the more remarkable, because in the interval of nearly thirty years since the appearance of his previous memoir, the facts subsequently published are at variance with his former views on this subject.

As the results of my inquiries are widely different from the conclusions of Cambessèdes, which have been almost universally adopted by botanists, it will be better to select from my several observations the analysis of the fruit of a species closely allied to the *Clusia Criuva*, Camb., upon the examination of which that able botanist principally relied, in the construction both of his ordinal and generic characters. Here the fruit is an oval drupaceous-looking capsule, 10 lines long and 8 lines in diameter; it is 5-celled, with 5 very thick fleshy valves, which break away by their margins from the edges of the partitions, and become rotately expanded, leaving a large erect 5-winged column, in the angles of which the seeds are fixed. Each cell contains about 12 seeds, enveloped in a thick mucilage, and these are attached horizontally by one extremity to the placentary column, in two longitudinal rows. The seed is of an oval form, about $\frac{1}{8}$th of an inch in length, and is slightly gibbous on the upper or dorsal side, the lower or ventral face presenting a prominent keel, extending from the base to a swollen point near the apex. The external tunic, at first thick and fleshy, and of an orange colour, forms when dried a thinner tough skin, and when it is scraped off, the keel seen on its ventral face is found to cover a bundle of fibres in the form of a raphe, one end of which proceeds from the stipitate base of the covering and the point of its attachment to the placenta, as well as to the body which it encloses, the other end terminating near the summit by a sudden reflexion, where it enters an aperture through the crustaceous integument of the seed: this is a hard, brittle shell, striately punctate, of an oval form, and a little flattened at the base, where, somewhat excentrically, is seen a very small point or cicatrix at the origin of the raphe-like cord: on the contrary or apical extremity, always somewhat on the ventral side, and around the opening through which the raphe-like cord penetrates the shell, is observed a prominent ring, radiately striated, forming a hollow cup: this outer shell is smooth within, and lined with a very thin free integument, that is contracted near the summit by a narrow neck of a darkish colour, by which it is suspended and connected with the extremity of the raphe-like cord: the solid nucleus filling the cavity of this integument is of a pale greenish colour, marked by numerous very distinct, prominent, parallel and longitudinal lines of an orange colour, which do not reach the base, but terminate round a flattened colourless space, like that seen in the outer shell, and in the middle of which a minute shining tubercular point is observed: the apex of the nucleus is distinguished by a short hemispherical nipple-shaped protuberance of a smaller diameter, which is divided to its base by a distinct transverse cleft into two equal portions, the bottom of this commissure on the ventral side corresponding with the dark-coloured

neck of the inner integument, as well as with the somewhat lateral aperture in the outer shell, and the termination of the cord already described; on making a longitudinal section of the nucleus, this cleft is more distinctly seen, and at the bottom of this commissure is observed a small prominent point, and also in the axis extending from this spot to the small tubercular point at the base is seen a continuous line, more or less narrow, somewhat curved, and of a more opake and whiter colour than the body of the nucleus: the principal mass is of a semi-crystalline hue.

This internal thickened line is what Gærtner considered to be the embryo of the seed, and the fleshy surrounding mass to be copious albumen. Choisy, Cambessèdes, and most other botanists, have considered the main body of the nucleus to be two large cotyledons agglutinated into one solid mass, the line of their junction being indicated by the curved line just mentioned, while they held the nipple-shaped protuberance to be the radicle. In the description above given, I have been careful to avoid the use of technical names in designating the several parts, until the whole evidence has been stated; but the inferences I have drawn from these facts, which I will here endeavour to substantiate, are, that the seed is enveloped by an entire arillus, with a raphe extending from the hilum, or basal point of its attachment to the arillus and placenta, to the process or cup-shaped ring surrounding the aperture situated near the geometrical apex of the testa, and through which the nourishing vessels of the raphe pass, to unite with the inner integument: the small cicatrix at the opposite extremity of the testa, near the hilum, must be considered as the micropyle. Most botanists will perhaps call this extremity the *base* of the seed, and correctly so, although others have considered the geometrical apex as the true *base*, because it was once the base of the ovule before it became reversed in its position by its anatropal development: the use of this term, unless accompanied by an explanation of the sense in which it is applied, leads constantly to error and confusion*. The existence of the internal chalaza in the contracted and thickened summit of the inner integument, and its connexion

* Great mystification is often created by the misapplication of the several terms *umbilicus*, *hilum*, *apex* or *base* of the seed, which are used in a contrary sense by different botanists; and even Richard, who may be regarded as a leading authority on this point, is not free from similar confusion. St. Hilaire, in his Monograph on the Brazilian *Violaceæ* (Mém. du Mus. xi. 446), accurately describes the structure of the seed in *Viola* to be carunculate at the point of its placentary attachment, which he calls the "*umbilicus*," and the corresponding point of the *testa*, the "*hilum*," to which the inferior radicle is directed, while the areolar "*chalaza*" is seen at the opposite extremity, or "*apex*." Prof. Kunth, on the contrary (Nov. Gen. et Spec. v. 368), describes the seed in *Viola* as being carunculate at the *apex* by which it is attached to the placenta, with a *basal* chalaza at the opposite extremity: the embryo is said to be inverted, with its *superior* radicle directed to the *hilum*. Here we observe that two of the highest authorities apply the same terms in a directly opposite sense; the one truly, as regards the point of the placentary attachment of the seed, considering that point as its base, whatever be its position in respect to the axis of the fruit: the other uses the same terms relatively to the direction which the seed may bear in regard to its position with the axis of the pericarp, which in the instance of *Viola*, being suspended from the placenta, gives a reversed attitude to all its several parts: if this loose glossology were admitted, how could we define the base and apex of the seeds, where they sometimes happen to be erect, horizontal, and pendent in the same cell?

Cambessèdes has fallen into an error of a similar nature in reversing the position of the seed in his representation of *Clusia Criuva* (Flor. Bras. pl. 65. figs. 8, 9 & 10), where the stipitate support is miscalled and delineated as an apical arillus, and his radicle (the true cotyledons) are seen at the *base*, instead of the *apex* of the seed.

with the raphe through the *diapyle* * or aperture in the testa, constitutes an important feature in this inquiry. The nipple-shaped protuberance in the summit of the nucleus, hitherto taken to be the radicle, appears to me, without the smallest doubt, as was first shown by Richard, to be the two cotyledons of the embryo, which, although small and short, are nevertheless quite distinct, and their relative position is indicated by the direction of the cleft, being placed right and left of the axis, or with their commissure pointed to the raphe: the main body of the nucleus, instead of being the confluent cotyledons, as hitherto supposed, must be a gigantic radicle, in the axis of which is imbedded the caulicle of the embryo, shown in the opake central line previously mentioned, terminated at its base by the shining speck before described, and at its apex by the plumule, which is seen protruding into the space at the bottom of the cotyledonary cleft. The minute external speck, which I consider to be the germinating point of the caulicle, is always more or less prominent, and of a green colour in the living state: this point does not exactly correspond in position with the micropyle of the testa, but is somewhat lateral in respect to it, and nearer the basal origin of the raphe.

Although this axile portion of the radicle is plainly distinguishable in numerous other less prominent cases, it has never been distinctly noticed. In *Pekea* the superiorly exserted portion of this process has been called the caulicle †, a name also given to the large germinating protrusion in the embryo of *Rhizophora*, but inappropriately, because that term is applicable only to the ascending system, or the elongating portion of the plumule above its junction with the cotyledons: all below this point belongs to the descending system, and in order to distinguish it from the main radicular mass, it may be called the *neorhiza*: it is in fact the growing portion of the elementary root, the more external mass of the radicle being inert, or at least serving only the purpose of albumen or of large fleshy cotyledons, in affording nutriment to the germinating parts of the embryo ‡.

* This word is proposed to denominate the distinct aperture often seen pierced through the substance of the osseous testa, and by which the raphe penetrates, to unite with the chalaza of the tegmen or inner integument of the seed, and is used in contradistinction to the *foramen*, a term applied to the orifice of the primine of the ovule, which afterwards becomes the *micropyle* of the seed: this last, in seeds produced from anatropal ovules, is situated at the extremity always opposite to that in which the *diapyle* is placed. In the case of *Clusia* above detailed, the *diapyle* is a very manifest aperture, filled with soft fungous matter; in some other cases it is closed by the osseous deposits of the testa, and is only recognizable as the point where the extremity of the raphe, when it is free, penetrates the testa. This must not be confounded with the *omphalode*, a term applied by Turpin to express the aperture in the centre of the hilum in antitropal seeds through which the nourishing vessels pass to promote the growth of the embryo; nor with the *caruncula*, a name used to express indiscriminately any excrescence or swelling upon the testa, whether about the strophiole, about the hilum, or about the micropyle, where, according to St. Hilaire, it is sometimes observed, as in *Euphorbia*, *Ricinus* and *Polygala*.

† This term (synonymous with the *tigelle* of the French botanists) is vaguely applied by some authors: thus Gaudichaud (Recherches sur l'Organographie, &c. p. 39) defines "la tigelle, ou ce qu'on nomme ordinairement la radicule dans les embryons; cette partie sert à la composition des tiges." By this is evidently meant only that ascending portion of the collar of the embryo, which I have above defined as the true caulicle, and which does not belong to the radicle, although continuous with it.

‡ It may be maintained by some, that Gærtner's view is correct in considering the great body of the radicle as an albumen, and the neorhiza as the radicle, both agglutinated into one mass; but this argument will not hold good,

I have already alluded to the existence of two somewhat different developments of the seed in the *Clusiaceæ*; the foregoing description affords an example of the one which includes all cases (as in the tribe *Clusieæ*) where a number of seeds are formed in each cell of the ovary, and where they are attached in a horizontal position by their base to the axile placenta. The other development occurs in those instances (as in the tribes *Tovomiteæ* and *Garcinieæ*) where only one seed is formed in each cell, and where this is fixed to the axile column in a vertical position by its ventral face. For reasons that will be offered in another place, I propose to exclude the *Moronobeæ* and *Calophyllcæ* from the Order. In the first case (the *Clusieæ*), the raphe, enclosed within the fleshy arillus, is seen to extend from the base to the apex of the seed, and is free from the testa; in the second instance the testa is thinner and more membranaceous in texture, and enveloped in an overlapping arillus, which is thicker and more membranaceous in substance; it has a large hilum upon its ventral face; the raphe, less discernible, is imbedded in the substance of the testa, where it spreads into numerous branching nervures, conspicuously extending over its surface: in the *Garcinieæ* we find a similar testa, enveloped in an entire, copious, more or less mucilaginous pulp; tolerably good figures of this development are given by Gærtner in plate 105, illustrating the seeds of *Garcinia*, and in several plates of Dr. Wight's 'Icones.' Were it not for the explanation afforded by the analysis of the *Clusieæ*, the structure of the embryo in the other tribes, *Tovomiteæ* and *Garcinieæ*, would not be so easily understood. During my residence in Brazil, I examined in a living state the fruit and seeds of different species of *Tovomita*, *Commirhœa*, and more especially of a plant which I have called *Lamprophyllum lætum*, the type of a genus very distinct from *Garcinia*, and comprising numerous species of South American and West Indian origin, among them the *Calophyllum Calaba* of Linnæus, and others associated with *Garcinia* and *Calophyllum*, which last genus I consider to be foreign to the Order. The analysis of the seed of *Lamprophyllum* will afford a good example of the second mode of development above referred to. The drupe is here about the size of that of *Calophyllum Calaba*, as figured by Jacquin (Stirp. Amer. tab. 165), and contains generally two, or often by abortion a single seed, about the size of the kernel of a hazel-nut, which is enveloped in a thick mucilaginous pulpy arillus: the testa is thin and brittle, marked by numerous veins branching from the ventral hilum, and it contains a solid nucleus of a firm and somewhat fleshy consistence, exhibiting in the apex a minute prominent nipple of the size of a very small pin's head, seated in a deep hollow depression, a little below the summit towards the ventral face; near the base, somewhat on the dorsal side, is seen another smaller speck, which is green and shining, exactly like that described in the nucleus of the *Clusieæ*. On making a longitudinal section, the main body of the nucleus is seen to be of a pale sulphur colour, studded with numerous small oblong ducts, which, when thus cut, copiously exude a deep yellow viscous juice: a slender terete neorhiza, exactly resembling

because we see in the *Clusieæ* that the neorhiza is traceable only to the nascent point of the plumule, that the cotyledons are wholly exserted from and an extension of the main body, and that many of the striæ or long tubular ducts, which extend from the base to the apex of the mass of the nucleus, are carried without interruption along the outer face of the cotyledons, proving the continuity of the one with the other; for were it of the nature of albumen, it would be in the form of an investiture of the embryo, not a prolongation of it.

that observed in the seeds of the *Clusieæ*, is seen in the centre, somewhat oblique with the axis, one extremity of which terminates in the minute nipple near the apex, and the other in the basal speck before mentioned: this latter spot is without doubt the germinating point of the root, the apical nipple is the plumule, the main body of the nucleus must be the radicle, and the cotyledons at first sight appear to be altogether wanting; but on examining more attentively the minute nipple-shaped process, this is seen formed of four diminutive fleshy imbricated scales, surrounding a central prominent point, which is concealed by the two inner and larger scales; the two outer decussating scales thus separated from each other, are smaller, shorter, and placed right and left of the ventral face, as in the cotyledons of the *Clusieæ*. This structure is so minute, that it requires the aid of a strong lens to distinguish it. It may be said by some, that the two outer scales form part of the plumule, and in such case the embryo would be truly acotyledonous; but it appears to me that they ought to be considered as the real cotyledons, not only from analogy, but because they agree in position with the cotyledons found in the *Clusieæ*, with their commissure directed to the ventral face. I have elsewhere pointed out the analogy of this structure to that of *Caryocar*, and it constitutes a curious physiological fact. The absence of cotyledons has long been recorded in plants of a low order of development, and is known to occur also occasionally in exogenous plants among those which are almost leafless, such as *Cuscuta*, *Vohiria*, &c., whence it has been argued, that the abortion of the cotyledons in the embryo is indicative of the future absence of leaves in the plants produced by the growth of such seeds. In the case of the *Clusiaceæ*, however, where the floral structure is of the highest order of development, belonging frequently to the largest trees of the tropical forests of both hemispheres, with copious foliage, large fleshy leaves, and rich in mucilaginous juices, the absence of cotyledons in the seed, or their reduction to microscopical proportions, offers an anomaly suggestive of many considerations upon the nature of the organs of vegetable reproduction.

This same internal structure of the seed occurs in every instance I have examined, and is confirmed by all the evidence obtainable from recorded authority, so that little doubt can exist that it is constant throughout the Order, with the exception of genera, which, for reasons to be mentioned in another place, I propose to exclude from the family. The evidence here alluded to exists in the drawings of Gærtner, to which I have already referred; in the rough sketch given by Plumier in his 'Pl. Amer.' tab. 257. fig. *g*, *h*, *i*, which shows a similar structure in the seeds of *Rheedia lateriflora*; Dr. Graham also thus describes the seeds of *Hebradendron gambogioides*, "cotyledons thick, cohering in an uniform cellular mass, radicle central, filiform, slightly curved," a structure which, though described in other terms, is substantially the same organization that I have related; Dr. Wight, in his admirable 'Icones,' gives other examples of a similar structure, in plates 118, 192 and 960; and Dr. Roxburgh exhibits the same facts in his 'Coromandel Plants.' These are the only positive details I find upon record, except the analysis of *Calophyllum*, to which I will revert at another time. All accounts therefore confirm the constant presence of that peculiar development in the axis of the solid nucleus of the seeds of the *Clusiaceæ*, which I have characterized as the neorhiza of the embryo; for our decision upon this point will determine the nature of the other parts of the nucleus, to which such

various attributes have been assigned. This determination is fortunately assisted by the drawings of Dr. Roxburgh, whose details, always accurately observed, are copied by Dr. Wight in his 'Icones,' where in pl. 192. fig. 12 & 13, is shown a seed of *Xanthochymus dulcis*, in a state of germination, together with a longitudinal section of the same: here is depicted precisely the same linear process (the neorhiza), which is throwing out a root from the basal speck I have described, while the apical nipple of this same process has simultaneously become extended considerably, carrying upward with it the leaflets of the growing plumule: from the lower part of the neck thus protruded, and beneath the two lower scales which I have designated as the cotyledons, a second rootlet is seen to sprout, tending first horizontally and then downwards. We have here unquestionable proof that the process in question is what I have called *neorhiza*; for were it the embryo imbedded in albumen, as Gærtner affirms, it would not throw out descending shoots at the upper portion as well as the base; nor would the same result follow if it were the radicle, according to the view of Dr. Graham. The fact is certainly fatal to the conclusions of Choisy, Cambessèdes, and other modern botanists, that the great mass of the nucleus consists of two confluent cotyledons, and that the mammæform apex seen in the seed of the *Clusieæ* is its radicle, even if this opinion had not been disproved by the structural appearances which I have already described, and which are still further confirmed by a more minute examination of its internal organization.

On placing a thin transverse slice of a seed of *Lipophyllum* (*Clusia*, Camb.) under the microscope, it will be seen to be of a reticulated texture, and composed of a number of small hexagonal cells filled with yellowish grumous viscid matter, except in the centre, across the line of the neorhiza, where the cells cease to be distinguishable: close to the periphery, and corresponding with the external striæ which I have described (p. 246), a circle of about fifty very conspicuous ducts is observed, each duct having a diameter three times that of the reticulated cells: they are separated from each other by one or two rows of the same kind of cells that fill the main area, the circumference of the nucleus being formed of a very thin epidermis lined with parenchyma. On examining another slice of the same seed, cut in a vertical direction parallel with the axis, a somewhat different appearance is manifested; the cells no longer seem reticulated, but form regular longitudinal channels, interrupted by transverse septa placed at distances nearly equal to their diameter, bearing the semblance of articulated tubes or muriform tissue; they cease to appear along the line I have designated as the neorhiza: the large ducts near the margin are entire and hollow tubes with simply striated surfaces, and are filled with a yellow secretion of a more fluid nature than that of the cells, though still somewhat viscous. The neorhizal portion appears formed of longitudinal and exceedingly minute lines, exhibiting a uniformly striated opake and whitish texture. I have observed, in the seeds of the genus *Quapoya*, a structure exactly similar to that just described, except that in addition to the external row, a few similar longitudinal ducts filled with yellow fluid appear interspersed within the main area. M. Cambessèdes, in his figure of *Clusia Criuva* before referred to, has depicted on the outer surface of the nucleus the same external striæ, but he makes no allusion to the circumstance in the text.

It is requisite to offer some observations upon the nature of the external covering of

the seed, and to determine whether we are right in considering it to be an arillus, as doubts have been suggested on this subject by some eminent botanists. In the *Clusieæ*, this consists of an entire coating, without the smallest fissure; it is fleshy, equal in substance, not very thick, and generally of a reddish or orange colour. In the *Tovomiteæ* (at least I speak from observation in *Tovomita* and *Commirhœa*, and Pöppig relates the same of *Chrysochlamys*), it is slit upon the dorsal face from top to bottom, with its fimbriated edges overlapping each other, so that when opened out, it appears like a flat sheet with the seed attached in its centre. In the *Garcinieæ*, the external coating is much thicker, of a more fluid and mucilaginous substance, generally edible, and quite entire, as in the *Clusieæ*. Notwithstanding the different aspect and texture of this covering in the two last-mentioned tribes, its nature cannot there be questioned, and it is quite fair to conclude that the precisely analogous development in the *Clusieæ* is, in like manner, a true arillus. It is, however, essential to determine this point beyond cavil, because in the *Hypericinæ*, *Marcgraaviaceæ*, and other orders, it has been held to be merely a thickened epidermis of the testa, while in the *Magnoliaceæ* it has been assumed to be the testa itself. In the latter family, where the seeds are generally suspended by long funicular threads, it forms a very conspicuous development, under the appearance of an entire, fleshy, scarlet-coloured covering, precisely similar to that of the *Clusieæ*, and where in like manner within it, on one side, somewhat pressed into its soft substance, is seen proceeding from the basal hilum to the apex a flattened raphe, the upper extremity of which is lost in a fungous spot filling the cavity of a distinct aperture pierced through the osseous shell,—a tunic which by most botanists has been regarded as the *testa*, but which, by some authorities, has been held to be the *inner integument* of the seed, called *tegmen* by Mirbel, and *endopleura* by DeCandolle. Endlicher was the first to suggest this idea, which he expresses in a very ambiguous manner; in his 'Genera Plantarum,' p. 837, he states that the seeds of the *Magnoliaceæ* have, in most cases, an external, fleshy, coloured *integument* covering a crustaceous *testa*, with its *raphe* situated between it and the *testa*, and terminated by a *chalaza* in its summit, but that sometimes there is no *outer integument*, the *raphe* in such case being found between the *testa* and *endopleura*. In this definition, Endlicher evidently designates by the term *chalaza*, the aperture in the summit of the *testa*, which I have called *diapyle*, and such misapplication of the term *chalaza* (a word, strictly speaking, confined to the peculiar thickening of the *tegmen* or *inner integument*, where it is connected with the *raphe* around the point in which all further trace of the continuity of the nourishing vessels ceases) has probably led to the error of considering the true *testa* to be the *tegmen* of the seed. In the diagnoses of the several genera of the Order (at least in the tribe *Magnolieæ*), the first-mentioned character is assigned in detail to each genus in succession; but as the latter very inexact feature (where the *raphe* is found between the *testa* and *inner integument*) is applied to no single genus, it was probably meant to refer to the *Illicieæ**, although this is nowhere explained or described. Dr. Asa Gray, however (in his 'Genera Pl. Un. St.' i. p. 60. pl. 23), adopts and amplifies this suggestion in unequivocal terms; stating that in *Magnolia* the seed is

* On some future occasion I will state my observations upon the seeds of *Drymis*, which present anomalous appearances worthy of notice.

exarillate, and he denominates the scarlet-coloured external tunic the *testa*, which preceding botanists have considered to be the *arillus*, while the hard crustaceous shell, called *testa* even by Endlicher, is designated by him as the *tegmen*. This he infers from the fact of having observed spiral vessels in the placentary attachment of the ovule (*loc. cit.* fig. 7), which he thinks "clearly demonstrates that the baccate exterior integument of the seed is formed of the primine of the ovule, and therefore is not an arillus*." Had this distinguished botanist actually traced the growth of this last-mentioned tunic in its different stages, from the primine of the ovule, he would have established an inexplicable fact, but this he does not appear to have done; simply therefore because the primine is the more exterior tunic of the ovule, and the arillus is the outermost coating of the seed, it does not necessarily follow that the one is the product of the other; and notwithstanding the argument of Dr. Gray, there is little reason to doubt that in *Magnolia* the scarlet envelope is due to a subsequent growth over the primine, as occurs in other numerous well-known cases. I would not, however, now presume to question the validity of an inference standing upon such high authority as that of my valued friend, without being able to offer reasons grounded upon observations made by me many years ago in Brazil, upon living seeds of *Talauma*, a genus closely allied to *Magnolia*. 1st. I found the thick outer tunic to consist of a fleshy or oily matter in distinct granules enclosed within a thin external epidermis, and an inner one of a similar nature; this is the usual texture of *arillus*, not of *testa*. 2nd. The coating called *tegmen* by Dr. Gray, and considered by him as the innermost integument, is in reality the intermediate envelope in *Talauma*; it is black in the living state, with a small basal hilum; a longitudinal furrow runs along its ventral face for the reception of the *raphe*, and a brown fungous scar, through which the *raphe* finds a passage to the interior, fills a hollow cup in the apex, where there exists a distinct aperture (the *diapyle*) for this purpose: this process Dr. Gray, following the example of Endlicher, considers to be the *chalaza*: the crustaceous envelope is thick and osseous in texture, bearing all the characters of a *testa*, and certainly none of those of an innermost integument of the seed. 3rd. The existence of a membranaceous *inner integument* around the albumen, first indicated by Gærtner, within the true *testa*, thickened and discoloured around its summit by a well-marked *chalaza*, where it is attached by a short neck to the fungous process that covers the *diapyle*, and where it unites with the

* St. Hilaire has expressed similar views in regard to *Euphorbiaceæ* (Leçons de Bot. p. 728), founding his notion upon the authority of Schleiden, who, although a very acute observer and a physiological botanist of the highest repute, is not always free from error in his conclusions, and who asserts that the external fleshy coating of the seed of *Euphorbia* is derived from the primine. I have examined a great many seeds of arborescent *Euphorbiaceæ* in Brazil, and have found them generally covered with a coloured fleshy arillus, having a distinct raphe extending from the apical hilum to the basal diapyle of the bony testa, and which cord constantly occurs between the testa and arillus: there always exists a more internal membranaceous integument with its basal chalaza. It is therefore clear in these cases, as in the instances alluded to in the text, that the nourishing vessels proceeding from the placenta through the funiculus to the foot of the primine, will, by the reversion of the ovule, necessarily have become extended with it, and produced along its surface; and it follows that the raphe, thus resulting and afterwards apparent as a free or imbedded cord, will manifest itself always upon the outer face of the testa (the product of the primine), and that whatever coating may posteriorly appear covering the raphe, such must be of subsequent and exterior growth, and therefore an arillus.

raphe, is a development wholly unnoticed by Dr. Gray, by Endlicher, or by DeCandolle; but it is an important feature, because it proves that the bony coating is the *testa*, and not the *tegmen* as has been inferred. 4th. The *raphe* proceeding from the hilum is wholly exterior to and free from the osseous coating, and interior to the outer tunic; and this is the constant position of *raphe*, when it is free, in regard to *arillus* and *testa*,—assuredly not in respect to *testa* and *tegmen*. 5th. As the *raphe* consists of the nourishing vessels originally existing in the funiculus or placentary attachment of the anatropal ovule, it could never have existed between the *primine* and *secundine*, but must have been, as Dr. Gray figures it, wholly exterior to the *primine*, and consequently, as we afterwards find it, outside the *testa*, which is the product of the *primine*; hence as the *raphe* is found in a free state, though partially impressed in its soft substance, within the external tunic, the inference is irresistible, that the latter must be of posterior growth, therefore *arillus*, and in this manner enclosing the *raphe*. 6th. We have thus the evidence complete, of the existence of the usual and distinct envelopes around the nucleus of the seed, viz.:—an *inner integument* with its apical *chalaza*, an intermediate hard *testa* with its corresponding *diapyle*, through which the nourishing vessels of the more exterior *raphe* penetrate, and the whole included within a scarlet-coloured soft *arillus*.

From all these facts we may safely infer, that the envelope, which is unquestionably an *arillus* in the *Garcinieæ* and the *Tovomiteæ*, must be of the same nature in the *Clusieæ*, and that which is *arillus* in the *Clusieæ* must be the same development in the *Magnoliaceæ*: that which is granted in the one cannot be denied in the other. Although it be true that the several envelopes of the seed in different families are not to be recognized alone by their consistency, which may be, contrary to general rule, more or less membranaceous, ligneous, cellular, or composed of oily or resinous granules according to circumstances, yet they may be determined by their relative position in regard to *raphe*, *chalaza*, *diapyle*, *micropyle*, *hilum*, &c., from which their true nature may always be inferred with greater certainty*.

* The want of precaution in attending to the nature of the nourishing vessels proceeding from the placenta and penetrating the different integuments, in order to promote the growth and perfection of the seed, has frequently led to a misconception of its real structure. These vessels present themselves in the shape of a raphe-like cord under three very different aspects:—1st. When the cord, originating in the base of the cell, terminates often at the opposite extremity in the hilum of the contained seed; it is then properly the *funicular cord*, of which the common Cherry affords a very good example: sometimes it is inappreciably short; in other cases, as in *Magnolia*, it forms a very long thread, by which the seed is suspended when it escapes from its cell. 2nd. When these vessels, existing in the form of a thread, either free and exterior to the testa, or partially imbedded in its substance, spring from the point of attachment of the hilum of the testa, and extending along its surface, penetrate its substance at a spot called the diapyle, to unite with the chalaza of the inner integument, which is invariably opposite to the cotyledonary end of the embryo; this is the well-known *raphe*. 3rd. When the vessels passing from the hilum penetrate the inner integument and extend in the shape of a thread beneath its surface, in order to attain the radicular (not the cotyledonary) extremity of the embryo; in this case they constitute the *suspensor*, which has sometimes been mistaken for a raphe; it occurs in *Tropæolum*, where its origin has been well illustrated and described by Dr. Giraud, in a memoir on the development of the embryo in that genus, published in the nineteenth volume of the Society's Transactions. The want of attention to the existence and position of the true raphe has often led to erroneous inferences in regard to the affinities of different genera, and among the *Clusiaceæ* may be cited the instance of *Calophyllum*. Gærtner (De Fruct. i. 200. tab. 43. fig. 1) gives an analysis of its fruit, where overlooking the existence of the raphe, he has mistaken the extra-

Connected with the issue of this question is that of the origin and mode of growth of the arilliform covering of seeds, which by St. Hilaire is considered to be of two kinds; one designated by him the *true arillus*, the other the *false arillus*; the former he defines as an envelope open at its extremity, while the latter entirely covers the seed*. This has been well discussed by Dr. Planchon, in an able memoir on the subject†, where he greatly modifies the views of St. Hilaire, and proposes to give to the false arillus the name of *arillode*. Under this point of view, both kinds of envelope are alike in colour, texture and form, being either gland-like, lobed, laciniated, more or less cupuliform, or entire and wholly concealing the testa; their difference consisting in this, that the arillus, whether abbreviated or entire, always covers the micropyle of the testa, while the arillode constantly exhibits a minute or larger opening in its surface, around the micropyle, which is never covered by it (*loc. cit.* p. 10), and he further points out the mode of distinguishing the one from the other. "Si cette ouverture (le micropyle) est cachée par l'enveloppe, ou si elle doit l'être, dans le cas où celle-ci serait prolongée, on a un véritable arille. Si le micropyle, au contraire, n'est pas recouvert par l'enveloppe, ou ne peut l'être même par cette dernière prolongée, nous aurons un faux arille du même genre que celui de l'*Euonymus*." It will be seen that St. Hilaire points to *Euonymus* as an instance of his true arillus: Dr. Planchon, on the contrary, selects that genus as offering the type of his arillode. He traces the distinction that exists between them from their different sources of origin, attributing the growth of the true arillus over the ovule to a gradual enlargement of the funiculus, and noticing its earliest appearance from a mere swelling of the umbilical cord to its gradual increment and ultimate development; but the arillode he states to be derived from an enlargement of the mouth of the exostome or foramen of the ovule, its margin being reflected and produced over the primine, thus growing upon it in the form of an additional tunic. In either case, whether this accessory coating be of the nature of arillus or arillode, it is clear, if it be entire, that the raphe must necessarily be enclosed within it. The arillus, according to this view, is found in the *Passifloraceæ*, *Dilleniaceæ*, *Anonaceæ*, *Samydaceæ*, *Turneraceæ*, *Bixaceæ*, *Sapindaceæ*, &c., while the arillode is conspicuous in *Celastraceæ*, *Cactaceæ*, *Malvaceæ*, *Büttneriaceæ*, *Euphorbiaceæ*, &c.: in this latter family, however, the peculiar caruncuioid swelling around the micropyle (I do not allude to the fungous strophiole) is called arillode, while that integument which I take to be the true arillus in that Order (note, p. 253) is considered by Dr. Planchon to be a mere epidermis of the testa. It would indeed be difficult to discriminate between a thin arillus and a thick epidermis, as both appear to be of the same nature, differing only in their relative thickness. The origin of the arillus is now well established, but

ordinarily thick testa for the endocarp of the putamen, and calls the inner integument its testa. I have observed, however, the existence of this cord springing from the point of attachment of the hilum to the base of the cell of the putamen, and extending along one side to the summit of the cell, where it penetrates the very thick testa, to unite with the inner integument at the cotyledonary end of the embryo. The very peculiar nature of this testa, together with the small inferior radicle, and the existence of two large distinct fleshy cotyledons in the embryo, added to other differences in the structure of the flower, and the peculiar venation of its leaves, all serve to remove this genus from the *Clusiaceæ*, its position being probably in *Lophiriaceæ*, as was long ago suspected by Prof. Lindley.

* St. Hilaire, Pl. Us. no. 43. p. 4.

† "Mémoire sur le développement et les caractères des vrais et faux arilles," &c. Montpellier, 1844.

that of the arillode, as indicated by the interesting researches of Dr. Planchon, requires to be confirmed by a series of more extensive and careful observations, before it be admitted as a settled fact. The most instructive and conclusive evidence of the origin and subsequent extraneous growth of the arillus over the ovule, has been adduced by Cambessèdes*; he found among the ripe seeds of *Casearia grandiflora* many that were incomplete; and here, although the anatropal ovule showed itself in a state of complete abortion, the arillus had grown over it to its full state of development, proving that where the ovule had ceased to grow, the increment of the funiculus was not stopped in its progress of extraneous production.

Among the instances cited and figured by Dr. Planchon of the development of the arillode, is that of *Clusia flava*, where he describes its ovules as presenting two short cupulary membranaceous appendages, one covering the fourth part of the ovule, the other much shorter and superimposed; and while he inquires, whether one of these cups be due to an expansion of the funiculus, and the other of the exostome, he seems inclined to infer that both proceed from an enlargement of the foramen of the ovule. Such an inference is opposed to the facts described in the foregoing pages, but his observation is worthy of attention, although it is more probable that the appearances he describes are those of a true arillus in progress of its development, the exterior swelling being perhaps that enlargement which I have described as the stipitate foot of the arillus. According to the views of Dr. Planchon, the exterior coating existing in the seeds of the *Clusieæ* must be a true arillus, because the micropyle, which I have mentioned as existing near the hilum of the testa, is wholly covered by that envelope. It is proper to notice that Cambessèdes distinctly asserts that the seed of *Clusia Criuva* is enveloped in its apex by a scarlet cupuliform arillus, in the work last referred to (p. 317. pl. 65. fig. 8), where it is figured upon the extremity of the seed contrary to that of the hilum, and connected with it by a raphe: this assuredly must be an error, made perhaps in transcribing the notes of St. Hilaire, who by such swelling probably intended to figure the cupuliform caruncular process surrounding the diapyle, which I have shown to exist in the same position in the summit of the testa: that such a mistake evidently exists, is proved by the circumstance of Cambessèdes having described and figured the arillus in the *apex* of the seed, instead of being at the *base*, as it would have been had it been in existence. Von Martius (Nov. Gen. et Sp. iii. 166) describes the ovarium of *Quapoya* (*Schweiggera*) as containing "ovula basi arillo vaginata," and Endlicher, upon no other authority than the above, states that the seeds of *Havetia* are "basi arillo subcarnoso laxè cupulæformi cincta," and he assumes upon no better evidence the same in regard to those of *Quapoya*, which in that genus Aublet affirms to be "pulpâ rubrâ involuta."

The facts which I have here brought together, relative to the structure of the seeds in this family, must in a considerable degree change our views of the affinities of the *Clusiaceæ*. They serve to bring the Order into close proximity with the *Rhizobolaceæ*, a relationship founded upon analogies in the floral structure, long ago pointed out by Cambessèdes†, but now rendered still more evident by the great similarity observed in their

* St. Hilaire, Flor. Bras. Mérid. ii. 232. pl. 126. fig. 11.

† St. Hilaire, Flor. Bras. Mérid. i. 323.

extraordinary embryonal development. In this last-mentioned family, the embryo of its exalbuminous seed exhibits, in like manner, a gigantic radicle furnished with exceedingly minute cotyledons; with this difference, however, that the cotyledons here are separated from the great body of the radicle by a slender free neorhiza or neck; but if we imagine the suppression of this neorhizal extension in the *Rhizobolaceæ*, and the close approximation of its minute cotyledons to its monstrous radicular mass, there would be little or no difference in the form of the embryo in the two families. At the same time that these circumstances tend to draw closer the affinities of the *Clusiaceæ* to the *Hypericaceæ* and *Marcgraaviaceæ*, they remove them to a considerable distance from the *Ternstrœmiaceæ*, with which Order they have been hitherto considered to be most intimately related. At present, I will do no more than indicate these considerations, as it is my intention to discuss this question more extensively upon a future occasion, when I treat on the general organography, floral structure, and generic features of the whole Order, restricted as I propose it to be. I will merely observe, that in the course of this investigation, I have met with many singular deviations from usual forms, and numerous interesting facts well deserving of record.

EXPLANATION OF THE PLATE.

Tab. XXVI.

Fig. 1. Seeds of *Lipophyllum latum*:—*natural size.*

Fig. 2. A seed of the same, seen on the ventral face, with the prominent keel which covers the raphe:—*much magnified.*

Fig. 3. The same, seen laterally.

Fig. 4. The same, with the arilliform covering removed, and the raphe separated, showing the testa with its nearly apical diapyle, and basal micropyle.

Fig. 5. Half of the testa of the same removed, showing the inner integument, with its apical chalaza.

Fig. 6. The inner integument, with its chalaza.

Fig. 7. Half of the inner integument removed, exhibiting the position of the enclosed embryo.

Fig. 8. Embryo seen laterally, showing the small cotyledons in the apex, and the prominent striæ upon its surface.

Fig. 9. The same, seen on its ventral face, exhibiting the commissure between the cotyledons.

Fig. 10. The same, viewed from the summit.

Fig. 11. Transverse section of the same, showing the external row of ducts which form the longitudinal striæ; the neorhiza is seen in the centre.

Fig. 12. Longitudinal section of the same, displaying one of the cotyledons, the gigantic epirhizal radicle enclosing the axile neorhiza, which is terminated at its upper extremity by the minute plumule, and at its base by its germinating point prior to its coleorhizal protrusion to form the root of the future plant:—*all also much magnified.*

Fig. 13. A seed of *Lamprophyllum lætum*, enveloped in its pulpy arillus.

Fig. 14. The same, with the pulp dried, and half of it removed, in order to show the enclosed seed.

Fig. 15. The testa seen on its ventral face, displaying its large hilum, and the branching nervures of its imbedded raphe.

Fig. 16. The same, seen laterally.

Fig. 17. The embryo seen on its ventral face, showing the minute plumule in the umbilicated hollow near its summit.

Fig. 18. A transverse section of the same, marking the central neorhiza.

Fig. 19. A longitudinal section of the same, with the axile neorhiza, and numerous viscous ducts distributed through the mass of the immense epirhizal radicle:—*all natural size.*

Fig. 20. A seed of *Tovomita rufescens*, showing on its ventral face the attachment of the arillus to the axile placenta of the fruit.

Fig. 21. The same, displaying the manner in which the free margins of the arillus overlap each other.

Fig. 22. The same, with the arillus removed, seen laterally.

Fig. 23. Embryo, with the testa removed.

Fig. 24. The same, cut longitudinally, to show the plumule and the neorhiza in the axis of an immense epirhizal radicle.

Fig. 25. Portion of the summit of the embryo, showing the minute plumule in the hollow of its apex:—*all natural size.*

Fig. 26. The plumule removed, showing the two very minute external cotyledons.

Fig. 27. A portion of the base of the embryo, showing the radicating point of the neorhiza:—*both much magnified.*

Fig. 28. A seed of *Commirhœa mecocarpa*, seen laterally, enveloped in its fleshy arillus.

Fig. 29. The same, exhibiting on its dorsal face the manner in which the free margins of the arillus overlap each other.

Fig. 30. The arillus removed and spread open, denoting the cicatrix where it is attached to the hilum.

Fig. 31. The testa seen laterally, showing the hilum and branching nervures of the imbedded raphe.

Fig. 32. The embryo, with the testa removed, seen on its ventral face, with its apical umbilicus.

Fig. 33. Longitudinal section of the same, cut through the dorsal and ventral faces, showing the immense epirhizal radicle enclosing the axile neorhiza, and its radicating point.

Fig. 34. Germination of the embryo of *Xanthochymus*, after Roxburgh, exhibiting the prolongation of the plumule, with its basal cotyledons, and showing one radicating shoot springing from the neck of the protruding neorhiza, and another from the basal point; half of the radicle is here removed to display the whole neorhiza, and the mode of its prolongation both upwards and downwards: the radicle thus appears to exert no other function than to afford nutriment to the growing neorhiza:—*all natural size.*